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Movement, home range and clustering in the European hare (*Lepus europaeus* Pallas) in The Netherlands

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Abstract

To examine aspects of dispersion in hares, data about movements and home range were collected from recoveries of tagged individuals as well as from radio-tracked animals. Most hares moved less than 500 m from the capture place, even the sucklings, and the mean home range size observed was 29 ha, showing a sedentary way of life. Displaced hares mostly could establish themselves near the place of release, and a low degree of agonistic behaviour to an introduced tame conspecific was observed.

Home ranges overlapped considerably, and at night clustering was observed. While in the twilight hares grazing gregariously showed less attentive interruptions compared with hares grazing solitarily, anti-predation behaviour was thought a function of clustering.

As from literature is known that under circumstances with poor food supply, such as in desert and in areas with deep snow cover, hares become more territorial during the reproduction season and more migratory in the winter, the results suggest that in our study areas food was not in short supply, presumably due to a high hunting pressure in autumn.

Introduction

Although in South-East Europe, after periods with heavy snow, groups of hundreds of roaming hares have been observed (Angermann 1973), roaming over large distances seems the exception in this species. Data collected by Andersen (1951), Rieck (1953, 1955), Szederjei (1959), Douglas (1970) and Pielowski (1972) showed that about 80 percent of tagged animals released on their capture place, were recovered within a distance of 3 km, and less than 10 percent were found more than 5 km away. Rieck (1953) calculated from his recoveries of tagged hares that the home range rarely exceeded 500 ha. Pielowski (1972) recovered tagged individuals in areas of about 350 ha, while he concluded from observations of the movements of hares being pursued, that hares are familiar with an area

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of about the same size. However, he also pointed out that a distinction should be made between the larger area covered by the hare's movements during its life time, and the several clearly defined areas, far smaller in size and occupied temporarily and periodically, situated within the boundaries of that total home range. By repeatedly shifting its area of activity, a hare would be kept informed of the situation within the total home range. The area in which Pielowski observed a hare during one day was on average 20 ha.

Merz (1976), following hares during a three month period of radio-tracking, and Schneider (1978), who collected data over periods of 0.5 to 1.5 years by direct observation, found total areas of activity of about the same size as the areas of daily activity observed by Pielowski (1972). Their data clearly point to a non-migratory way of life, from which one might expect territoriality. Indeed, Rimathé (1977) and Schneider (1978) found indications that the movements observed in subadults were not only due to an urge to explore, but were also caused by intolerant behaviour from adults, possibly their own parents. On the other hand, Douglas (1970) and Szederjei (1959) found that most of the leverets were able to establish themselves in the area they were born in, and even within the home range of the parents. Also contrary to territorial animals, resident hares are often observed in groups, by day as well as at night. Although several authors showed an influence of field conditions on the distribution of hares (a. o. Brüll 1973; Fiechter 1975; Frylestam 1976; Jezierski 1968; Merz 1976; Pielowski 1966; Rimathé 1977), Merz (1973, 1976) observed clustering at night which he could not explain by a preference for certain vegetation, but in his opinion could have a social function. The same was suggested by Pielowski (1966) and Jezierski (1968) dealing with clustering in the daytime.

Since literature about spacing out and social clustering does not conform, we collected additional data about the size and changeability of the home range, the movements of adult and juvenile hares, the behaviour after introduction to unknown area and about clustering and its possible function.

Material and methods

Capturing, tagging and recoveries

Size and changeability of the home range were examined from recoveries of tagged individuals, as well as by direct observation in the field. For both methods animals had to be captured. Leverets, unless they were found by accident, were located by searching meadows about three quarters of an hour after sunset, using a binocular provided with a spotlight. At that time the leverets left their hiding places in order to gather for nursing (Broekhuizen and Maaskamp 1980). Attempts were made to capture the leverets by using a hoopnet after they had been nursed and the doe had withdrawn. In total 99 leverets were tagged with a numbered aluminium chicken wingmark. Beside the number, the name and phone-number of the institute were also punched on the tag, to facilitate the notification of recovery. Leverets were aged by means of body weight and length of the hind foot (Broekhuizen and Maaskamp 1979). After tagging they were released on the same spot where they were captured.

Adult hares were captured by chasing them into vertically placed long nets. No drugs were treated for handling. Nearly five percent of the animals captured were lost through shock and accidents. Apart from the wing tag in the ear already mentioned, a numbered plastic tag of the "Dalton-rototag" type was connected to the other ear. During the years 1968–1978 637 adult hares were captured and tagged at ten different locations, 132 of which were released at the spot they were captured, and 505 were released on fields 10 to 90 km away from their capture place. Capturing took place in the second half of December and the first half of January, just at the beginning of the reproduction season.

Hares were considered as adult, when they were aged as six months or older from the stage of ossification of the distal epiphyseal cartilage knob of their ulna (Broekhuizen and Maaskamp 1979). Recoveries from our own field work were neglected, in view of the biased chance of notification.

Measuring of the home range by direct observation

Home ranges of 13 hares (8 females and 5 males) were determined by radio-tracking. Technical data on radio-transmitters, their connection to the animal and the receiving units used were described earlier

(Broekhuizen et al. 1979). For these hares the ear tags and the radio-collar were plastered with reflecting "Scotchlite" tape, to facilitate observation at night using the spotlight.

Since it was almost impossible to track hares during the whole night, it was done either from dusk till midnight or from midnight till morning. Generally one hare was tracked intensively. We attempted to locate it by triangulating the radio or by spotlight view every quarter of an hour. The location of other radio-collared hares in the vicinity was determined at the beginning and at the end of the observations, and in the time in between as far as possible.

Home range was defined according to Burt (1943): "that area which is traversed by the animal (male) in all its activities as gathering food, resting, mating, caring for young. It excludes occasional sallies outside that area and shall be calculated for a specific period of time". The size of the home range was determined according to the minimum observation area method of Odum and Künzler (1955), connecting the outermost observations to the smallest convex figure in which all the other observations are located.

The periods in which the home ranges of the various hares were determined, are given in table 1. The hares numbered as 1–6 and 10–13 lived in the area "Cortenoever" about 4 km south of Zutphen, a town in the valley of the river Yssel (52.06 N; 06.13 E). This area was mainly used for dairy. The hares 7–9 lived in the "Noordoostpolder" (52.45 N; 05.13 E), mainly used for arable farming.

Behaviour after introduction in unknown areas

Besides the recoveries of hares that had been moved, the behaviour after introduction in an unknown area was also studied from a female hare raised in captivity, which was released in September, at the end of the reproduction season, in the area "Cortenoever". The animal was radio-collared for swift locating, and since it was familiar with human presence and activity, it could easily be observed from a car. Special attention was given as to whether the introduction induced agonistic behaviour in the established hares which finally resulted in the introduced hare being chased away.

During the first three days after introduction, the animal was observed continuously, and afterwards from 5.00–10.00 p.m. In the 14th night after introduction, the introduced hare was predated by a polecat.

Determination of clustering

As clustering can also be the result of nonuniformity of the habitat, we studied the distribution of hares on very uniform, cultivated meadows. During May and June 1977, ten meadows in the area "Cortenoever" were observed twelve times between 6.00 p.m. and 7.00 a.m. This was done from a car, using binoculars with a spotlight. The meadows, the location of which is indicated in fig. 2, were selected for their appropriately low vegetation. In these meadows several points were marked with reflection-tape to facilitate the location of the hares observed. The spots on which they were first observed, were marked on a map. The distances between the marked hares observed per meadow area were compared with random distributions of the same number of hares on the same area.

Influence of clustering on alertness

The influence of clustering on the alertness of the hares was quantified by measuring the frequency of attentive interruptions during grazing, i.e. when hares stopped grazing to look around briefly. Observations were made between two hours before and one hour after sunset, and between one hour before and two hours after sunrise, from a car and without using a spotlight so as to prevent any disturbance of the hares' behaviour. Protocols were recorded on tape, for being worked out afterwards. Grazing bouts shorter than four minutes were not taken into account.

The observations were made on the same meadows used for studying clustering, as far as the grass was short enough to observe grazing and attentive behaviour in detail. The observations were restricted to hares located 50–100 m from the road, to enable making detailed observations without influence by road-traffic.

Results

Size and changeability of the home range

The size of the home ranges of the 13 radio-tracked hares during the total periods of observation are shown in table 1. The mean size was found to be 29 ha. The relation between the length of the observation period and the size of the home range turned out to be insignificant ($r = 0.29$; $n = 13$; $p. = 0.05$), and the individual differences are distinct.

Table 1

Observation periods and home ranges of 13 radio-collared hares

C = Cortenoever, N = Noordoostpolder

hare	sex	area	observation period	period of intensive observations	number of observation-nights 'intensive'	'incidental'	home range (ha)
1	♀	C	31 July'73 - 30 Aug.'73	1 Aug.'73 - 30 Aug.'73	15	17	25.5
2	♂	C	31 July'73 - 4 Oct.'73 19 Jan.'74 - 15 Feb.'74	1 Aug.'73 - 4 Oct.'73 19 Jan.'74 - 15 Feb.'74	31 13	15	59.5
3	♂	C	25 Aug.'73 - 8 Feb.'74	25 Aug.'73 - 20 Sep.'73	16	43	12
4	♀	C	25 Aug.'73 - 4 Dec.'73	25 Aug.'73 - 27 Nov.'73	45	20	16
5	♂	C	18 Oct.'73 - 6 Dec.'74	18 Oct.'73 - 6 Dec.'73	25	21	13.5
6	♀	C	19 Jan.'74 - 15 Feb.'74	19 Jan.'74 - 15 Feb.'74	13	2	7.5
7	♀	N	15 Jan.'75 - 7 Feb.'75	20 Jan.'75 - 5 Feb.'75	4	9	13.5
8	♂	N	15 Jan.'75 - 3 Apr.'75	20 Jan.'75 - 21 Mar.'75	19	12	30
9	♂	N	15 Jan.'75 - 16 May '75	20 Jan.'75 - 15 May '75	27	9	72
10	♀	C	15 July'75 - 31 Oct.'75	22 July'75 - 10 Aug.'75	16	23	23
11	♀	C	24 Jan.'76 - 16 Apr.'76	2 Feb.'76 - 9 Apr.'76	10	14	57
12	♀	C	14 Jan.'76 - 16 Apr.'76	2 Feb.'76 - 9 Apr.'76	10	15	13
13	♀	C	14 Jan.'76 - 16 Apr.'76	2 Feb.'76 - 9 Apr.'76	11	14	30
							Mean: 29

The cumulative increase of the home ranges of the hares numbered 1–6 in table 1 is shown in fig. 1^A, while for the same animals fig. 1^B shows the area size which would be used till the end of the observations. For reasons of comparison, for both graphs only data obtained from nights during which the animals were tracked intensively were used. The figures show an increase of the total home range due to utilisation of areas not previously in use, and a decrease of the area which was observed to be used after that. This indicates shifts of the activity area which involves abandoning parts of the area. Such shifts may be gradual as well as abrupt. Not only new areas are involved, but also areas occupied earlier can be taken in use again.

Home ranges of hares tracked simultaneously sometimes showed an extensive overlap, as is illustrated in fig. 2 for hares studied near "Cortenoever". Hares with overlapping home ranges were repeatedly observed close together, also when they were of the same sex.

Movements in adults and young

Fig. 3 shows the distances between the places of release and recovery of individually tagged hares, in relation to the time involved. The location of the place of recovery was not always exactly known, especially when the hare was shot during a drive. Of the hares recovered within one kilometer from the place of release, those for which it was certain that the distance was less than 500 m, are indicated separately.

From 132 adult hares released on the spot where they had been captured, 24 (18 %) were recovered (fig. 3^A), of which 58 % were shot and 4 % killed by traffic. Nearly all the recoveries concerned animals which moved less than 1 km from their place of release, and for 58 % that distance was certainly less than 500 m. From the data it can be concluded that movement does not increase with age.

From 99 leverets, estimated at 5 weeks old maximum age and supposedly still being nursed, 23 were recovered (fig. 3^B), of which 56 % were shot. No traffic victims were reported. Nearly all the movements found were less then 1 km, and for two third certainly less than 500 m.

The data indicate that also in young hares movement does not increase when they grow older. Movement of the young does not seem to differ from adults.

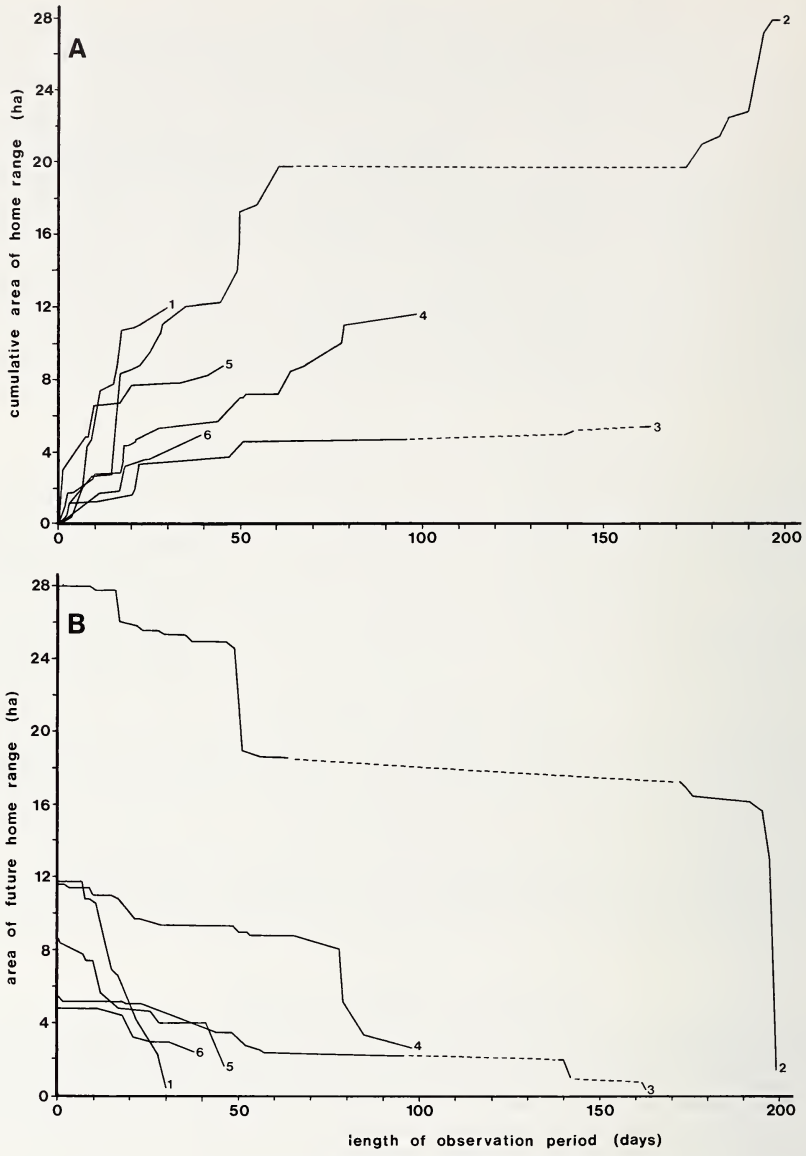

Fig. 1. Areas of realized (A) and future (B) home range in the course of the observation periods of the radio-tracked hares 1–6 from table 1, based on data from nights of intensive observation

Movements among introduced hares

From 505 introduced adult hares, 90 (18 %) were recovered (fig. 3^{C}), of which 70 % were shot and 19 % killed by traffic. Only 54 % of the recovered animals moved over more than 1 km and 9 % over more than 3 km. The data indicate that movement does not increase with time, so it is likely that the added movements in introduced hares mainly occurred just after releasing. The relatively high percentage of traffic victims also indicated movement before the animals were settled.

Fig. 2. Home ranges of radio-tracked hares in the area "Cortenoever", numbered as in table 1. The pastures from which clustering data were collected (table 3) are shaded

In fig. 4, the bearings indicate the direction and distance of migration related to the direction of the place of origin. A tendency of migration into the direction of the place of origin cannot be observed.

Interactions between an introduced and indigenous hares

Table 2 summarizes the observations of encounters between a released hare raised in captivity and indigenous hares during a fortnight just after releasing. Apart from this, we observed the hares 13 times passing by within 7 m of each other, without any obvious interaction.

From table 2, no distinct difference in behaviour between the introduced hare and the indigenous ones can be concluded. No chasing away of the introduced hare occurred, and the hare stayed in the area in which it was released.

Clustering

The comparison between observed distributions of hares on the meadows in the "Cortenoever" area and simulated random distributions is summarized in table 3. Out of 81 observations the observed distances were smaller than the simulated ones on 59 occasions, and they were larger 22 times. Since the difference is significant (sign test on observations and Monte Carlo simulations: $T = 37$; $n = 81$; $p < 0.01$) it may be concluded that hares at

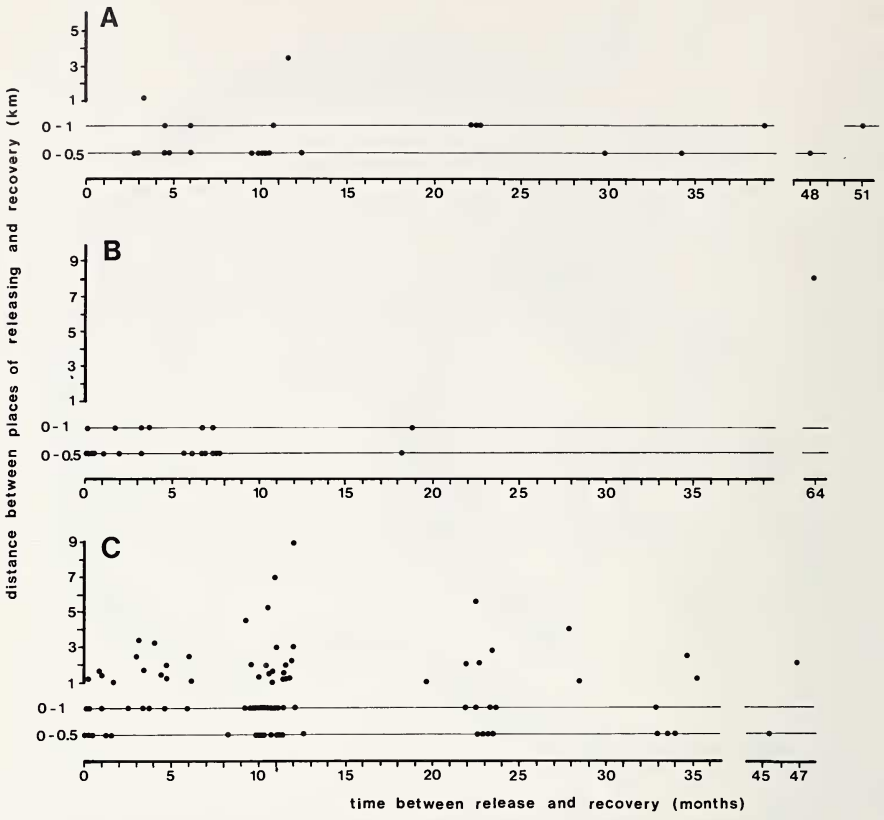

Fig. 3. Distances between the places of release and recovery of tagged hares, related to the time passed between release and recovery. A: tagged as adult, B: leverets tagged in their suckling phase, C: tagged as adult and released in a strange area

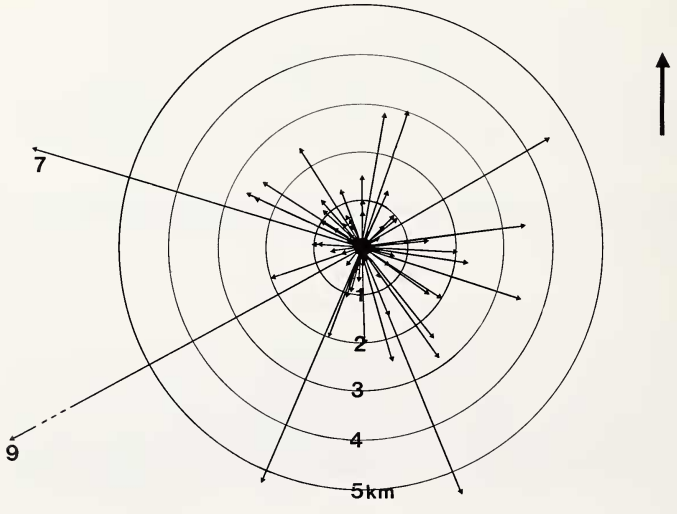

Fig. 4. Distance between release points (centre) and place of recovery (point of arrow) in displaced hares, with the bearings of migration related to the direction of the place of origin (arrow right)

Table 2

Behaviour in 19 encounters between a female hare released from captivity and conspecifics living in the wild

behaviour	hare released from captivity	'wild' hares
contact sought	9	10
sniffing at the conspecific	2	4
following each other	8	10
encircling the other one without approaching	6	3
leaping	0	2
aggressive behaviour (boxing, kicking, biting)	3	3
breaking off the meeting by going away	7	10
breaking off the meeting by flight	1	1

Table 3

Observed distribution of hares on pastures near Cortenoever (Fig. 4), compared with simulated random distributions

field (a)	number of observations (b)	total number of hares (c)	mean sum of distances to the nearest neighbour per observation simulated (d)	observed (e)	numbers of positive (f) and negative (g) difference between (d) and (e) (f)	(g)
a	12	94	485.8	246.4	10	2
b	6	15	290.5	208.9	4	2
c	4	17	305.3	241.5	3	1
d	8	30	277.2	160.9	7	1
e	6	21	290.7	194.9	4	2
f	7	29	289.0	299.3	5	2
g	7	25	393.9	200.8	6	1
h	11	54	246.2	214.0	5	6
i	11	73	376.4	264.1	7	4
j	9	50	221.3	156.9	8	1
Total	81				59	22

night are more clustered than could be expected from a random distribution. During the observations, no indications were obtained that clustering was bound to a particular condition or usage of the meadows, such as height of the grass or the presence of cattle. Only within 10 m from the road relatively few hares were observed.

Frequency of attentive interruptions during grazing

For describing the distance between two grazing hares, three categories were distinguished, viz. 0–7 m: hares grazing gregariously; 8–30 m: hares grazing in open clusters; more than 30 m: hares grazing solitarily. The observed frequencies of attentive interruptions within these categories are shown in fig. 5. A distribution is made between observations made around sunset and those made around sunrise. From the figure it can be concluded that solitarily grazing hares showed a higher frequency of attentive interruption than grazing hares in open clusters, whilst in the latter category the frequency exceeded that of hares grazing gregariously. Also at dawn the solitarily grazing hares showed the highest frequency of looking up. Differences between hares grazing in open clusters and those grazing gregariously were not observed, due to increased alert behaviour in the gregarious hares. It is likely that this increase is connected with a higher rate of sexual interactions in the morning, as found by F. Oomen-Kalsbeek and K. Noordam (unpubl. data).

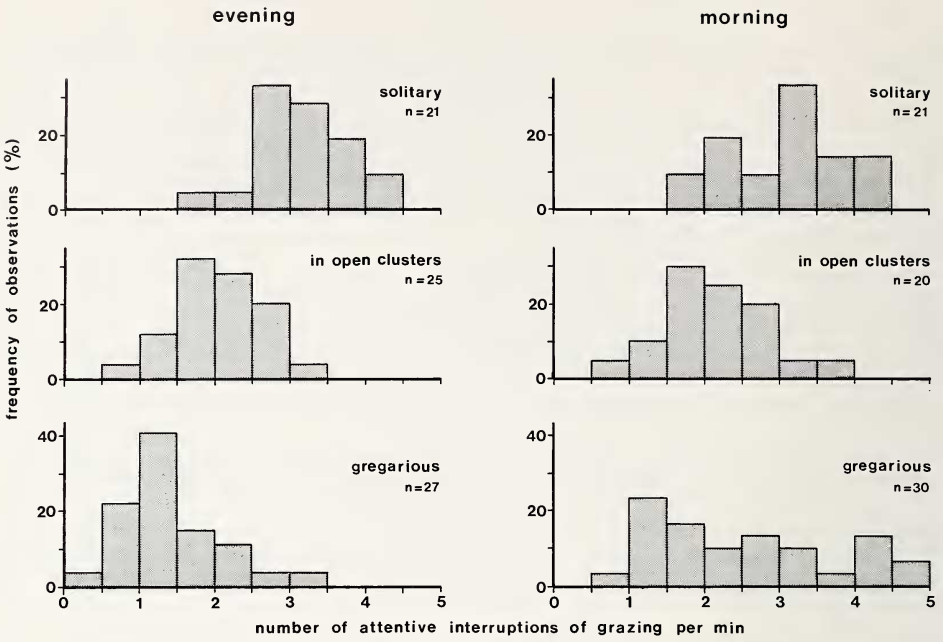

Fig. 5. Distribution of the number of attentive interruption of grazing per min in hares grazing solitarily, in open clusters and gregariously. *Left:* observations from two hours before till one hour after sunset; *right:* observations from one hour before till two hours after sunrise

Discussion

The collected data clearly indicate that in The Netherlands hares are very sedentary, even though their home range is not a fixed area. Occasionally the activity area is shifted. This, however, does not result in a continuous extension of the total home range, which is in agreement with the idea of Pielowski (1972), that the home range "contains several clearly defined areas, far smaller in size and occupied periodically, situated within the boundaries of the whole home range". However, the size of the home ranges we observed was on average about ten times smaller than that mentioned by Pielowski (29 ha versus 300 ha), and more in agreement with the home ranges observed by Merz (1976) and Schneider (1978).

From fig. 1^A it is likely that, where the observation periods varied from a few weeks to several months, the home ranges had not reached their ultimate size in all cases. Nevertheless we found no significant correlation between the total home range size and the length of the observation period, indicating that in most of the home ranges a large part of the ultimate size had been covered within a few weeks. This is in agreement with the recoveries of tagged hares, which also show that over longer periods and in other areas, most hares do not move more than 500 m and migration over more than 1 km is exceptional. This also holds for juveniles and sub-adults. Observations on dispersion of leverets after being nursed show that their radius of action can be several hundreds of meters at the end of the suckling phase (Broekhuizen and Maaskamp 1980). This indicates that the ultimate home range can already be reached during the suckling phase, and that generally juvenile hares do not need to migrate to become residents.

Home ranges of neighbouring hares, also when they are of the same sex, can greatly overlap (fig. 2). This, and the low degree of agonistic behaviour, even towards newly

introduced hares, indicates a high degree of tolerance within the home range area. Therefore, the greater tendency to leave the place of release in introduced hares (fig. 3) is unlikely to be caused by antagonistic behaviour of indigenous conspecifics, or by 'homing', as was found in some introduced hares by Jezierksi (1968) (fig. 4). As the greater moving distances in the former mainly occurred immediately after release, they are more likely to be a response to being caught and transported, or, as Pielowski (1972) expressed it, to be caused by shock.

The distribution of hares on meadows in the "Cortenoever" area showed an underdispersed clustered pattern. This may reduce the risk of predation, because it enables the perception of signals from conspecifics during twighlight and in the dark, when spotting of potential predators is most difficult. The function of the clustering behaviour was not studied, but the lower frequency of attentive interruptions during grazing in the presence of conspecifics indicates a decreased need for attention.

The combination of a non-migratory way of life, a low degree of intolerance, and a tendency to cluster does not always occur in hares. Angermann (1973) mentioned roaming groups of hares in South-East Europe during periods of heavy snowfall outside the reproduction period. Lindlöf (1978) observed aggressive dominance ranks in hares feeding from a hay stack when snow cover was deep. In *Lepus americanus* it was shown that when food was short, juveniles were expelled by adults and that immigrating adults more successfully settled than juveniles when the food supply was artificially increased (Windberg and Keith 1976). These studies all indicate that the food supply determines behaviour and spatial distribution.

The behaviour and spatial distribution of the hares we studied suggest that food shortage was not involved. This may hold for most of The Netherlands, because nearly all hare populations are hunted. Consequently, before winter starts and before the reproduction season a substantial part of the populations will be eliminated. Besides, in The Netherlands long periods with thick snow cover were exceptional in the last decade. Hence, the food supply is unlikely to be the limiting factor in population regulation.

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Zusammenfassung

Ortsveränderungen, Aktionsräume und Gruppierungen beim Feldhasen (Lepus europaeus Pallas) in den Niederlanden

Zur Untersuchung verschiedener Aspekte der Verbreitung des Feldhasen wurden Ortsveränderungs- und Lebensraumdaten gesammelt an Hand von Rückmeldungen markierter Individuen sowie durch Verfolgung der Bewegung von Hasen, die mit Sendern versehen waren.

Die meisten Hasen, auch Säuglinge, wanderten weniger als 500 m vom Markierungsplatz. Die mittlere beobachtete Lebensraumgröße war 29 ha. Dies deutet auf eine gewisse Standortstreue der Tiere hin.

Versetzte Hasen siedelten sich meistens in der Nähe der Aussetzungsstelle an. Nur selten wurde aggressives Verhalten ortsansässiger Hasen diesen ausgesetzten Tieren gegenüber beobachtet.

Die Lebensräume verschiedener Individuen überschneiden sich bedeutend. Nachts wurden Gruppierungen beobachtet. Da während der Dämmerung gesellig äsende Hasen weniger Aufmerksamkeitsunterbrechungen zeigten als allein äsende Tiere, wird vermutet, daß diese Vergesellschaftung teilweise als Feindvermeidungsverhalten anzusehen ist.

In der Literatur wird beschrieben, daß in Gebieten mit schlechten Nahrungsverhältnissen – wie in der Wüste oder in schneereichen Gebieten – Hasen während der Fortpflanzungszeit territorial sind und im Winter mehr wanderlustig werden. Die Ergebnisse dieser Untersuchung zeigen hingegen eine bleibende Standortstreue der Tiere. Diese läßt vermuten, daß in den von uns untersuchten Gebieten kein Futtermangel auftritt. Möglicherweise spielt dabei der hohe Jagddruck im Herbst eine Rolle.

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